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A NEW DIPLOPOD GENUS FROM GUATEMALA, CLOSELY RELATED TO DESMONUS, AND ITS EFFECT ON THE VALIDITY OF THE FAMILIES DESMONIDAE AND CYCLODESMIDAE (POLYDESMIDA: SPHAERIODESMIDAE)

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The species of Diplopoda are still so poorly known that the unusual is commonplace, particularly in collections from tropical regions, but despite having become somewhat inured to the unexpected I was astonished upon recently discovering abundant material of two milliped species that O. F. Cook had collected in Guatemala and identified as "*Desmonus*, n. sp." These specimens were found hidden in a large jar of Sphaeriodesmids making up part of the huge backlog of unidentified myriapods which has accumulated at the U. S. National Museum for more than 70 years, and were kindly loaned to me for study by Dr. Ralph E. Crabill, Associate Curator in the Division of Insects.

Despite the striking superficial resemblance of the new species to *Desmonus earlei* Cook and its congeners, they differ in so many ways that full generic rank must be admitted as necessary. Aside from their interest from both systematic and zoogeographic points of view, these creatures are also singular in casting light on the origin and significance of the curious segmental cavities previously considered characteristic of *Desmonus* and a few related genera.

Hybocestus, new genus

Type species—*Hybocestus octonodus*, new species (here designated).

Diagnosis—A genus of small, relatively slender sphaeriodesmoids, the length about four times the greatest width, in which the paranota of segment 3 are much the largest, the metatergites of segments 5 to the penultimate are provided with a transverse ridge bearing 6 or 8 conical tubercules, and segments 4 to the penultimate with rudimentary cavities at the base of the paranota. Male gonopods very simple, the coxae with a moderately distinct apophysis, and joined by a narrow transverse sternal remnant; telopodites simple, without accessory processes, the seminal groove running out to the tip of a long flagelliform tibiotarsal portion. Anterior legs of males without knobs or glandular

openings, but the femora and postfemora of legs 1-7 conspicuously enlarged, and the coxae of legs 3-6 produced into distinct conical lobes.

Remarks—The obvious similarity of this genus to *Desmonus* is noteworthy, considering the fact that related species and genera occurring between Texas and Guatemala are rather dissimilar in body form. We have two alternative choices to make on the basis of existing knowledge. Either *Hybocestus* and *Desmonus* represent terminal convergence at two extremities of the range of the ancestral stock, or they represent relicts of the original widespread prototype, with loss of ornamentation and other modifications occurring in specialized species evolving more rapidly in the region between them.

The generic name is derived from the Greek *hybos,* hump-backed + *kestos,* a girdle, the latter being especially appropriate in the sense of its extension into the Latin *cestus,* a knobbed contrivance worn on the fists of gladiators.

Species—Two, both from Guatemala.

Hybocestus octonodus, new species

Figures 1-4

Type specimens—Male holotype and female paratypes, U. S. Nat. Mus. Myriapod Type No. 2594, from Coban, Baja Vera Paz, Guatemala, collected in May, 1904, by O. F. Cook.

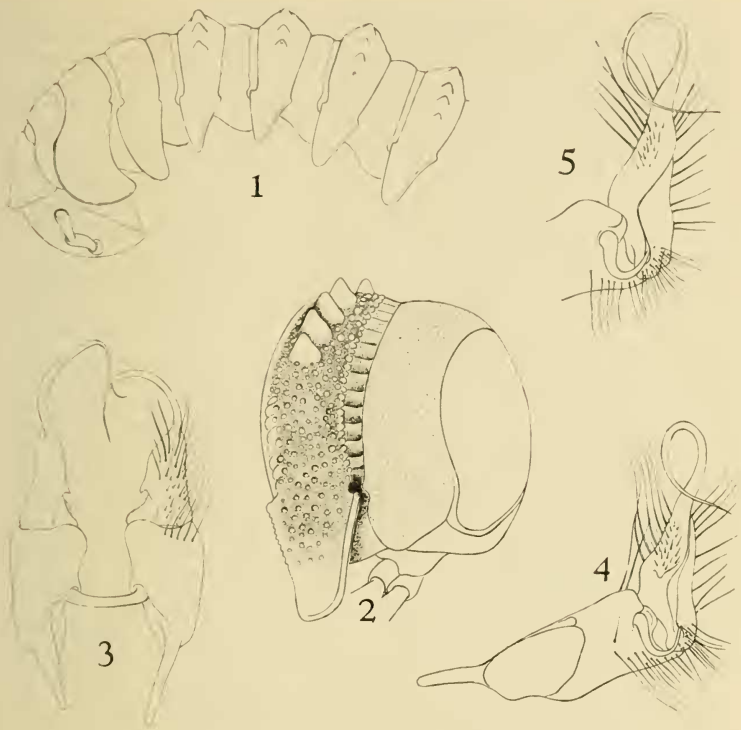
Description—With the characters of the genus. The following notes were made from the holotype after removal of all adherent dirt and debris:

Coloration uniformly testaceous, the tubercules and larger granules grayish white, legs yellowish.

Body slender, composed of head and 19 segments, capable of rolling into a compact flattened sphere, widest near the anterior end, tapering gradually back to 16th segment, thence abruptly to end. Length, ca. 11.0 mm., width, 2.7 mm.

Head fairly large, slightly wider than collum, moderately and evenly convex, the vertex smooth and glabrous but for two pairs of long paramedian vertigial setae, the innermost seta of each pair set distinctly lower on the head than the outer; surface of head below level of antennae becoming densely setose. Genal surfaces continuing the convexity of the frons, not medially swollen to form a subantennal ridge, laterally sloping off to a straight, thin, immarginate edge. Interantennal isthmus slightly broader than length of 1st antennal article but much narrower than length of 2nd; lower part of vertex without a median carina (such as reported by Loomis for several species of *Desmonus*) but with a broad flat elongate area set off by two indistinct grooves which extend dorsad from inner angles of antennal sockets and appear to converge abruptly about the level of the vertigial setae.

Antennae long and slender, extending caudad nearly to caudal margin of 3rd segment, all of the articles setose but most distinctly so distally, where the terminal four are invested with (1) dense, short setae, almost pubescence, (2) numerous more widely spaced and longer setae, and (3) an apical whorl of even longer sensory hairs. Antennae slightly compressed distally, the 6th article largest and longest, somewhat fusiform; 7th small and bluntly conical, with 4 long slender sensory



cones. Outer sides of articles 5 and 6 (perhaps also 7) with small, rounded, apical sensory areas. Lengths of articles in descending order: 6-2-3-5-4-1-7.

Collum subtrapezoidal, twice as wide as long, the anterior and posterior margins nearly transverse but the latter turned forward laterally; anterior corners rounded and depressed somewhat. Surface of collum smooth, with broad, low, faintly convex areas each with a median seta, four across the caudal margin, one on each side along the lateral margin, and two paramedian near the center of the collum.

2nd segment smooth, its paranota slender and enclosing collum, extending cephaloventrad as far as its anterior corners; both margins of the paranota slightly turned up to impart a somewhat flatly concave effect; dorsum of segment with a series of 8 setae along the caudal margin and out onto the paranotal bases.

3rd segment with greatly expanded paranota, these about twice as wide as those following, metatergites of this and all subsequent segments finely but densely granular, the prozonites smooth. Surfaces of these subsegments concordant at a narrow suture line; the 8 transverse setae of the metazonite near the midlength of the subsegment instead of near the caudal margin.

Segments 4 and 5 similar in shape, but former entirely smooth and flat, while the metazonite of the latter is elevated above level of prozonites and carries a median transverse series of 3 distinct high conical tubercules on each side of the middorsal line, and a much smaller tubercule on each side about halfway from the outermost large tubercule to the level of the paranotal bases.

Segments 6-17 subsimilar, the prozonites and metazonites separated by a deep constriction which becomes narrower and deeper on the lower sides, and which is ornamented by a series of subcontiguous ovoid pits. Surface of prozonites smooth and polished, that of metazonites beset with profuse, erect, conical microtubercules which accumulate a coating of dirt and organic debris in the living animals; the transverse dorsal series of large processes increasing in size and acuteness back to the 17th segment where they are at least twice as high as their basal diameter. Paranota relatively small and set low on sides, arching slightly ventrolaterad and then directly ventrad, the ends vertical; those of segments 5 and 6 acutely pointed, from segment 7 on caudad first becoming rounded and then truncate with the anterior corners obtusely-angled, the posterior acutely-angled. Anterior and lateral edges of paranota very thin and smooth, the posterior edge ornamented with a series of 8 to 12 or more denticles which increase in size toward the body. Anterior margins produced gradually cephalad toward the body, culmnating in a blunt lobe or *tragus* (a new term, selected with reference to the similarity to the tragus of the mammalian ear) which almost contacts the adjacent surface of the prozonite across the deeply impressed interzonal groove; the posterior edge also produced caudad at the base into an acute lobe which, when the animal is coiled, overlaps the tragus of the following segment.

Segment 18 reduced in size, its dorsal processes very low but still evident and discrete. Segment 19 small, profusely studded with coarse, boletoid granules, a large paramedian setiferous tubercule on each side near the middle, and provided with 6 long setae along the caudal edge. Basal half of segment nearly vertical, the distal half very slightly flared outward. Profile of 19th segment in ventral aspect slightly acute medially rather than evenly rounded.

Anal valves flat, each with two long medially directed setae, hypoproct large, subtriangular, longer than wide, the sides convex. Median length of hypoproct greater than the line of contact between the anal valves.

Pleural and sternal areas completely glabrous and smooth, the interzonal groove conspicuous and deep except in its course in curving forward in front of the anterior legpair, level of prozonite elevated above that of metasternum. No podosternal development, the legs attached to coxal sockets virtually flush with the sternal surface, the coxae of each pair in contact medially but well-separated from those of the other pair. Stigmata very small, ovoid, not auriculate, on the anterior lateral side of each coxal socket. Length of prozonite at midventral line about 2/3rds that of metazonite.

Legs long and slender, the coxae nearly glabrous but the distal articles moderately setose, especially the tarsus. Joints in descending order of length: 3-6-2-4-5-1. Pregonopodal legs somewhat shorter and

heavier than the others, the femora and postfemora of legs 1-7 distinctly enlarged, but not provided with any ventral lobes or glandular openings. Coxae of 2nd legs produced into long slender conical processes extending back between coxae of 3rd pair, the sternite of 2nd legpair pivoted on pleurotergite on each side and freely moveable. Coxae of legs 3-6 produced ventrad into conspicuous subtriangular lobes, those of pairs 3 and 6 separated, of 4 and 5 almost in contact.

Gonopod aperture very large and transverse, occupying most of sternum of 7th segment, the prozonite reduced to a mere narrow vestige about 1/8th the length of the opening, the metazonite reduced to a strip just wide enough to contain the coxal sockets of the 9th legpair, which are widely separated. Aperture not margined except at its lateral ends where the segment is produced into prominent subhemispherical lobes.

Gonopods freely moveable in the aperture, not attached to its edges, the coxae cylindrical and elongate, with a prominent apophysis just above insertion of the solenite, and with several long macrosetae just below it. Coxae connected by a slender but well sclerotized sternite, its apodemes largely fused with the coxae and remaining with them upon separation. Telopodite not definitely resolvable into distinct regions but basally enlarged and with long slender setae near insertion of the solenite, the mesial surface takes the form of a short ridge terminating in an acute basally directed spur, beset with short stiff bristles and bordered by a lateral row of long, slender macrosetae. Telopodite distally drawn out into a long acuminate flagelloid process describing a complete circle or nearly so, without any trace of accessory branches or processes. Prefemur of gonopod without indication of a prefemoral process.

Hybocestus plagiodon, new species

Figure 5

Type specimens—Male holotype and female paratypes, U. S. National Museum Myriapod Type No. 2593, from Tree Aguas, Guatemala, collected on March 30, 1906, by O. F. Cook.

Description—Superficially similar in most structural details and sexual characters to the type species, differing from *octonodus* in the following particulars:

Size considerably larger, the holotype 3.2 mm in width, a large female paratype 15 mm in length and 3.4 mm in width.

Body composed of head and 20 segments instead of only 19. Head considerably less setose on frons and clypeus, the genae with distinct flattened margins. Interantennal isthmus much broader than in *octonodus*, as broad as length of 2nd antennal article; lengths of the articles in descending order: 6-5-2-4-1-7, as opposed to 6-2-3-5-4-1-7.

Surface of collum finely granular instead of smooth. Segment 5 with 3 flattened tubercules on each side, those at the middorsal line in contact basally; the 3rd tubercule outward very small in relation to the paramedian series, halfway from it to the paranotal bases is a 4th, even smaller tubercule which is conspicuous chiefly because it carries a visible seta. Tubercules of segments 7 and 8, and 15 through 18 largest, those of segments 9 through 14 distinctly smaller, and in going caudad

on the body, the tubercules tend increasingly to slope caudad (hence the specific name) rather than remaining perpendicular on all segments as in *octonodus*.

Interzonal groove broad and very shallow, provided with oblong pits only far down on sides; metazonites very abruptly elevated from posterior margin of the groove. Posterior edges of paranota with about 15-20 small dentate tubercules, as against 8 to 12 in the other species.

Telson, as seen in profile, sloping evenly to the edge instead of the distal half distinctly flared outward.

Male gonopods very similar to those of the type species, but considerably larger; the femoral ridge less pronounced and the corresponding area somewhat more strongly expanded outward.

Comparative morphology of the lateral cavities

The genus *Desmonus* was originally based in part on the presence of deep circular pits at the anterior base of the paranota, extending from the 3rd to the penultimate segment. In the subsequently described *Desmoniella* (Loomis, 1943) the cavities were found in the proper position but only on segments 4 to 10 inclusive. This discovery alone compelled the recognition of some mutability in the character, and the Mexican genus *Peridysodesmus*, which is similar to *Desmonus* in gonopod structure, apparently lacks the cavities altogether. With *Hybocestus* we gain some insight into the mode of formation of the structures. As already remarked in the preceding description, the anterior edge of the paranota is bowed cephalad in going toward the body and the anterior basal part of each paranotum is thus produced into a projecting subtriangular lobe for which the name *tragus* was suggested. In both species of this genus the tragus extends distinctly cephalad over the interzonal groove, which itself is accentuated at the paranotal base, and virtually meets the adjoining surface of the prozonite. It would require but little further modification to affect a complete junction and fusion of the two areas, thus leaving the interzonal groove bridged over to form a circular tunnel. This in fact is the condition in *Desmonus*, as can be seen from specimens boiled in KOH to clean off the dirt, although here the basal part of the paranota is turned in sufficiently to close off the ventral end of the tunnel.

Do these cavities contain the ozopores? This point has been in doubt since Cook's time, and cannot be resolved at this time with complete assurance. However, specimens of *Hybocestus* have been cleaned with strong caustic, then decalcified in acid, dehydrated through alcohol, and mounted in balsam, and such preparations have been studied under oil immersion without any trace of pores being detected. Doubtless the pores are absent in this genus, and inferentially so in *Desmonus*, although the study of serial sections will be desirable for confirmation.

On the other hand, it is well worth mentioning at this point that ozopores do occur in the genera *Sphaeriodesmus* and *Cyclodesmus*, both stated by Cook (1898) to be poreless. Perhaps the location of the pores, on the reduced and incurved surface of the metazonites, plus their small size, caused them to be overlooked by earlier workers. In the two genera mentioned, the ozopores are located just dorsad to and in front of the base of the paranota in front, normally concealed by the caudal

margin of the preceding segments. Such a position for the pore is by no means unusual, however, as it is characteristic of most of the Oriental *Pterodesmidae* where it may even be on the ventral side of the paranotal base!

On the basis of this information, the family "Cyclodesmidae" (= *Cyclodesmus*) was credited as having pores in a key to families in the "Checklist of the Millipeds of North America" although the statement was pronounced false by a recent reviewer of that work who presumably relied upon old literature rather than personal examination of specimens.

The Status of the Families Desmonidae and Cyclodesmidae

Within recent years the number of species of polydesmoid millipeds related to *Desmonus carlei* has been greatly augmented by a variety of animals many of which depart in one way or another from the original characters attributed to the genus and to its family Desmonidae. Since most workers are still content to follow the old existing classifications in their haste to erect new species, it seems appropriate that this occasion be taken to review the status of the Desmonidae in the light of existing knowledge, even though some of the named genera and species are known only from very meagre descriptions.

The foundations of our knowledge of American onisciform polydesmoids were laid by O. F. Cook in 1898, at which time he recognized five families separated to a considerable extent by the relative sizes of the anterior segments and their paranota. Although Cook's taxonomic perspicuity was far better than average in the recognition of groupings and affinities within the Diplopoda, it must be recalled that in the five families alluded to, he was able to study specimens of but ten species, and some of the families were based exclusively on the characters of single species.

Cook himself remarked that his arrangement and key to families was an artificial one, ". . . the forms included not composing a natural group . . .," but it remained for Brolemann to suggest that the Sphaeriodesmidae, Cyclodesmidae, and Desmonidae were related to the Chelodesmidae, while the affinities of the Oniscodesmidae and Cyrtodesmidae lay instead with the polydesmid families. This system was followed by Pocock in the Biologia Centrali-Americana, but in the latest summary of the Polydesmida, the Count von Attems (1940) combines all onisciform polydesmoids in the single family Oniscodesmidae, admitting, however, two subfamilies on the lines suggested by Brolemann's dichotomy.

The Desmonidae was erected primarily on the basis of "the possession on each segment of a deep cavity located at the base of the carina in front." From the superficially similar genus *Cyclodesmus* (which formed the basis of a family Cyclodesmidae), *Desmonus* was further separated by having the surface of the segments granular-hispid, instead of smooth, even, and polished; and in that the paranota of the 4th segment are larger than those of the 5th instead of subequal as in *Cyclodesmus*. These two genera (and "families") were separated by Cook from the related Sphaeriodesmidae solely by relative sizes of the anterior segments and of the antennal articles.

So long as only one or a few species were known for each family, the

diagnostic characters used by Cook remained useful and valid. With passing time, however, new forms have been described which virtually demolish the original distinctions, as shall be discussed at this point.

At the time *Desmonus* was described, Cook was puzzled by two enigmatic species which he knew only from the literature, but admitted nonetheless as the types of two genera: *Cylionus* and *Cyphodesmus*. *Cylionus*, which Cook proposed for *Sphaeriodesmus gracilis* of Humbert and Saussure, was placed in the Sphaeriodesmidae but with the admission that most of its characters indicated closer affinity with *Desmonus*. *Cyphodesmus* Peters, based on *Oniscodesmus mexicanus* Saussure, was regarded as related to *Desmonus* although being several times larger than *D. earlei*, and differing in various other ways.

In 1910, Filippo Silvestri very briefly diagnosed and figured two remarkable new genera from eastern Mexico, without allocating them to a particular family. Of them, *Taphrodesmus* was provided with lateral "pits" in exactly the position they occur in *Desmonus*, but differed from that genus in lacking transverse rows of tubercules and in having the 4th and 5th segments largest instead of the 3rd. Silvestri's second genus, *Peridysodesmus*, differed from *Desmonus* in lacking lateral pits and transverse rows of tubercules, and in having the 4th segment as large as the 3rd, but the gonopods are basically similar to those characteristic of *D. earlei*.

In 1943, H. F. Loomis erected still another genus, *Desmoniella*, in which the male gonopods are virtually identical with those of *D. earlei*, and in which the lateral pits are present although not on all of the body segments. *Desmoniella*, however, is completely smooth dorsally and the 2nd segment is essentially as large as the 3rd.

Finally, with the description of *Hybocestus*, we are provided with species which, if known only from females, might understandably be regarded as congeneric with *Desmonus earlei*, so great is the general concordance in body form and proportions. Yet the genus departs from *Desmonus* in sexual characters, as well as in the more primitive development of lateral cavities which indicates something of their evolution into the form which characterizes the North American genus.

I think the conclusion to which we are compelled by existing information must be that the characters originally stipulated for the family Desmonidae are at best generic in value, insmuch as they are shared in various combinations (pits, dorsal ornamentation, size of anterior segments, and form of gonopods) by members of seven apparently valid and obviously related genera.

What, then, is the status of the name Desmonidae? On the basis of Cook's original key (1899: 452), *Taphrodesmus* goes into his Sphaeriodesmidae and *Peridysodesmus* into the Cyclodesmidae, yet both are closely related to *Desmonus*. The basic structure of the gonopods, particularly retention of a distinct sternal remnant, is characteristic of all three of Cook's "families" here considered, as well as of many primitive genera in chelodesmoid families. *Desmonus* and *Sphaeriodesmus* even share, in addition, virtually the same configuration of the 1st legpair of males, with the femora dorsally arched and provided with a basal tubercule or spur on the ventral side.

Pocock (1909: 117) has already combined the families, remarking

in his introduction to the Sphaeriodesmidae, "I include in this family the genera which Cook referred to the Sphaeriodesmidae, Desmonidae, and Cyclodesmidae, because the genera *Sphaeriodesmus* and *Cyclodesmus* appear to be linked to a certain extent by *Cylionus*, and because the essential feature upon which the Desmonidae were separated from the Cyclodesmidae is not known to occur in the one Central-American genus. Cyphodesmus, referred by Cook to the Desmonidae." Pocock tentatively retained Cyclodesmidae as a subfamilial designation, solely, however, on the basis of segmental size and shape, a character which we now know to be subject to much variation even in closely related forms.

Perhaps the single character which might afford a major dichotomy is the relative size and shape of the prozonites. In *Desmonus* and *Hybocestus*, at least, they are not strongly reduced and even ventrally are nearly as long as the metazonites. In *Sphaeriodesmus* and allied genera, the prozonites are quite small even on the dorsal side, and are virtually obliterated on the ventral side. What the relationship of the two subsegments may be in the numerous other genera concerned, I have no direct knowledge, and this matter must await future treatment. *A priori*, however, it does not seem likely that the character will prove to be much more stable than other details of body form. For the present, I can find no justification either in gonopod configuration or external characters for the continued recognition of the names Cyclodesmidae and Desmonidae on either the family or subfamily level, although some groups of genera in the Sphaeriodesmidae may share enough characters in comon to be thought of as desmonid or cyclodesmid.

In its new and more inclusive sense, the family Sphaeriodesmidae comprehends some 16 genera (some of uncertain validity) restricted to America north of Panama. The largest genera tend to inhabit discrete regions, viz., *Sphaeriodesmus* in the Central American highlands, *Desmonus* in southern United States, and *Haplocyclodesmus* in the Greater Antilles.

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Figure 1. *Hybocestus octonodus,* n. sp., lateral aspect of head and first 9 body segments, the distension owing to maceration of the specimen in caustic which has also caused the head to be far more exposed than under normal conditions. Figure 2. The same, an enlarged drawing of a midbody segment seen in a slightly oblique cephalolateral aspect, to show microsculpture of the cleaned surface, and relationships of the paranotal tragus to the interzonal groove. Figure 3. The same, gonopods in cephalic aspect, showing relationship of coxites to the sternite; setae omitted from left gonopod. Figure 4. The same, left gonopod in mesial aspect. Figure 5. *Hybocestus plagiodon,* mesial aspect of left gonopod of holotype. Figures 3, 4, and 5 drawn to the same scale.